

of late Woodland. This is paralleled in the tempering material which is sand and grit in the early stages and crushed limestone and shell in the later ones. Up to this stage there is no complexity in vessel shapes and form, and such embellishments as lugs, handles and feet are lacking.

TECHNOLOGICAL AND ARTISTIC ACTIVITY

POTTERY COMPLEX:

Manufactured by means of the coiling system

Manufactured by molding, rare

Tempered with:

Sand

Crushed quartz (Figure M)

Crushed limestone (Figure P)

Crushed shell, rare

Deep bowl shapes dominant

Wide-mouthed jars, present

No handles, lugs or feet

Lips are simple

Rims are straight

Rims occasionally partially punctuated with nodes or pustules on the interior, throat area, of vessels (Fig. 1, R', R'')

Drill holes below lips (Fig. 1, N)

Net-impressed (Fig. 1, A, B, C, D, N)

Fabric-impressed (Fig. 1, G, O, Q)

Cord-wrapped paddle impressed (Fig. 1, H, I, J, K, L, M)

Plain smoothed (Fig. 1, P, R'')

Basket impressed (Fig. 1, F)

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PALEONTOLOGY.—*The morphology and classification of the oldhaminid brachiopods*. ALWYN WILLIAMS,¹ Glasgow University. (Communicated by G. Arthur Cooper.)

The grotesque nature of that short-lived but widespread group of brachiopods including *Oldhamina* Waagen and *Leptodus*² has long been a source of palaeontological interest and has led to many conflicting interpretations of the morphology and habit. Before Waagen's masterly exposition (1887) of the morphology and affinities of the group the occasional specimen obtained from the marine Permian of China and India were so confusing that de Koninck described *Oldhamina* as a bellerophon and Kayser named *Leptodus* in the belief that it represented part of a fish skeleton.

¹ I record with pleasure the stimulating and helpful discussions I have had with Prof. T. N. George and Mr. G. Owen, both of Glasgow University, on the subject matter of this paper.

² The use of *Lyttonia* Waagen, 1887, in place of *Leptodus* Kayser, 1883, is without warrant.

In the past 50 years a number of important papers, notably by Fredericks (1925), Watson (1917), Wanner (1935), and Licharew (1932), have not only substantiated Waagen's conclusions but also added greatly to our knowledge of the diversification and derivation of the group so that now there is no doubt that although the oldhaminids are exceptional in a number of characteristics they were derived from the normal strophomenoids and are but unusual members of that group.

Oldhaminid peculiarities are manifold. The shell is disproportionately inequivalve, the hinge-line together with the articulatory apparatus is rudimentary and the muscles (as judged from the muscle scars) were correspondingly degenerate and often asymmetrically developed, the brachial valve

is typically highly lobate and the pedicle valve equipped with a complementary septal apparatus. But unusual as these features are the shell structure of the brachial valve appears to be the most radical departure from that of normal brachiopods.

SHELL FORM AND STRUCTURE

In all articulate brachiopods the shell, excluding the periostracum, is composed of two layers, an outer lamellar layer of constant thickness consisting of a mosaic of calcitic platelets and an inner fibrous layer of variable thickness built up of fibrous calcite. Work on the relationship between the shell and mantle in modern *Terebratulina* to be published jointly with G. Owen in the near future has shown that the differentiation of the shell layers begins at the mantle edge (Pl. 1, Fig. 1). The lamellar layer is deposited only by a few epithelial cells forming the tip of the outer lobe, the deposition of the fibrous layer begins immediately behind this narrow lamellar zone and is carried on to a varying degree by the outer epithelial layer of the mantle over the entire shell surface. Thus all internal processes and protuberances such as the terebratuloid loop are composed only of fibrous calcite and are deposited by enveloping invaginations of the outer epithelial layer of the mantle.

The shell of the oldhaminid pedicle valve (Pl. 2, Figs. 6, 7) is like that of any other brachiopod. It consists of an outer lamellar layer, and an inner fibrous layer traversed as in all strophomenoids by spicules of cryptocrystalline calcite which do not penetrate the lamellar layer but protrude through the innermost fibrous layers to give the internal shell surface a tuberculate appearance.

The brachial valve (Pl. 2, Fig. 2) however appears not to possess this twofold differentiation of the shell, for the outer lamellar layer is almost completely absent, the entire shell anterior to a small apical triangular area being composed only of fibrous calcite so that the external and internal surfaces are pierced by spicules. The absence of the lamellar layer over so large an area is not known in any other brachiopod and calls for a reinterpretation of the nature and growth of the brachial valve.

If analogy with modern terebratuloids is valid and in strophomenoids, too, those structures which are composed only of fibrous material were deposited within invaginations of the outer

epithelium, then that part of the oldhaminid brachial valve which is also composed of fibrous calcite was strictly internal and formed no part of the protective shell. In this event most of the structure hitherto identified as the brachial valve is no more than an internal skeletal support to a highly lobated mantle infold.

The brachial valve which in normal brachiopods is a part of the enclosing protective covering to the viscera and mantle is thus vestigial and obsolescent. It is represented by the small obtusely triangular portion of the shell situated apically and consisting of the usual outer lamellar layer and inner fibrous layers. It forms only the lobes of the degenerate cardinal process and the posterior part of the denticular sockets (Pl. 1, Figs. 3-5).

This interpretation is not as far-fetched as first impressions convey. Comparable developments in the strophomenoids are found in both the thecideids and the plectambonaceids whose strongly elevated platforms, deposited by the outer epithelium, are developed for the support of the lophophore. In the plectambonaceid *Lep-telloidea musca* Öpik (cf. Figs. 6, 7 of Pl. 1) the lophophore platform is so pronounced that it protrudes well into the interior for over half the length of the shell as a bilobed pseudopunctate plate diverging from the brachial valve just anterior to the cardinalia. The difference between such a development and that of the oldhaminids lies in the disproportionate size of the oldhaminid internal plate in comparison with the brachial valve the growth of which was arrested at an early stage of development.

The extraordinary development of the oldhaminid brachial valve and internal plate possibly occurred in the following manner. During the earliest stages of growth both lamellar and fibrous layers were laid down by the mantle which advanced from an initial locus of growth lying immediately posterior to the cardinal process and expanded laterally to cover an obtusely triangular area. Such a structure is reminiscent of an obsolescent interarea and chilidium but hardly homologous with them for the direction of growth was the reverse of that governing the deposition of a true interarea and chilidium. The mantle edge did not advance beyond the base of the triangular lamellar layer; but as growth proceeded the outer epithelial layer continued the enlargement of the incipient cardinalia and an inwardly directed plate-like ridge, the latter

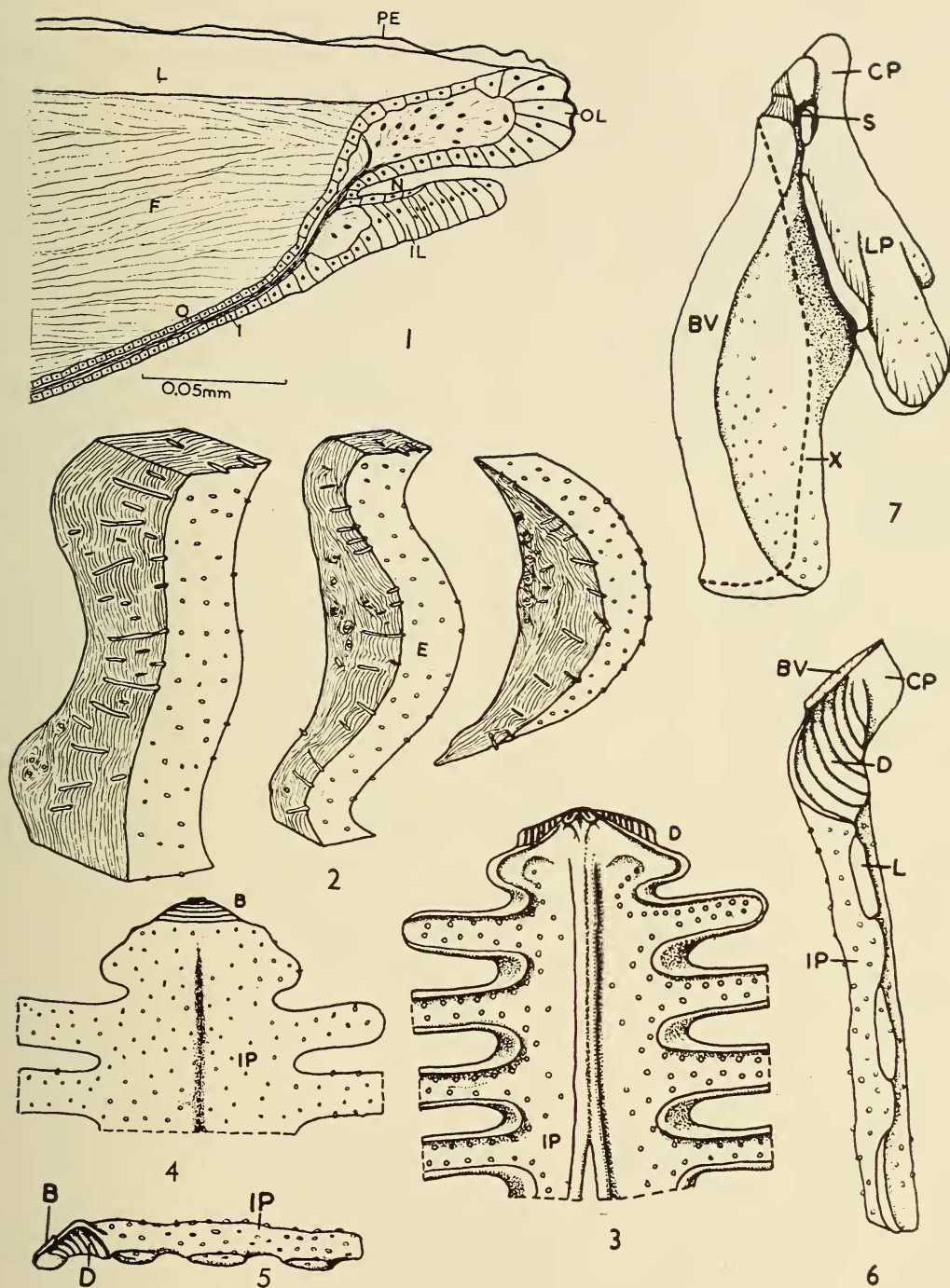


PLATE I

FIG. 1.—Radial section through the mantle edge of *Terebratulina* sp., Crinan Loch, Scotland, showing the relationship between the shell and the mantle lobes: F, fibrous layer; I, inner epithelium; IL, inner lobe; L, lamellar layer; N, setal groove; PE, periostracum; O, outer epithelium; OL, outer lobe.

FIG. 2.—Structure of a lobe of the brachial internal plate of *Oldhamina decipiens* Koninck as reconstructed from serial sections of specimen BM. 18646, Permian, Salt Range, India: I, internal surface; E, external surface. (× 10)

FIGS. 3-5.—Internal, external, and lateral views respectively of the posterior portion of brachial valve and internal plate of *Leptodus* sp. Permian (Word), W. Texas: B, vestigial brachial valve; D, sockets for dental areas; IP, internal plate. (× 3)

FIG. 6.—Enlargement (× 6) of Fig. 5 for comparison with Fig. 7 representing a lateral view of *Leptelloidea musca* Opik, Middle Ordovician, Baltic Provinces (× 7): BV, brachial valve; CP, cardinal process; D, socket for dental areas; IP, internal plate; L, lobe; LP, lophophore platform; S, socket; X, external profile of brachial valve.

encased in an epithelial sac, expanding anteriorly to form the internal plate. General oldhaminid morphogeny would lead in the subsequent development of the internal plate to the early appearance of a median incision by the accelerated growth of the submedian areas, and later, in phylogeny as well as ontogeny, the appearance of the lateral lobes.

In addition to imparting rigidity to the infold of the dorsal mantle, the internal plate probably gave support to the lophophore, a conclusion already advocated especially by Watson (1917) and Wanner (1935). The most primitive oldhaminid known is the upper Pennsylvanian *Poikilosakos* Watson, immature specimens of which possess a subcircular internal plate with a median incision (cf. *Cardinocrania* Waagen). If the lophophore was adherent to the periphery of such a plate it closely resembled the schizolophus so characteristic of many brachiopods. Moreover if the lobation of the internal plate was accompanied by a corresponding lobation of the lophophore it assumed the familiar pattern of the ptycholophous stage.

The shell composition of the oldhaminid brachial valve then, suggests that the brachial valve proper is a vestigial apical triangular structure, whereas the greater part of the shell consists of a lobated plate ensheathed in mantle tissue and giving support during life to a schizolophous or ptycholophous lophophore. The oldhaminid brachiopods were therefore functionally univalves (Pl. 2, Fig. 8).

The oldhaminid pedicle valve was normally developed to form a protective covering to the viscera and the ventral mantle lobe by which it was deposited; although it must be noted that, since the brachial valve and associated internal plate lay well within the periphery of the pedicle valve, a considerable area of the mantle must have been exposed.

The structure of the posterior portion of the pedicle valve is however exceptional. The apex of the valve is usually malformed through attachment, but it is evident that in place of an interarea there existed a small triangular patch of lamellar calcite which lay immediately posterior to the vestigial brachial valve (Pl. 2, Figs. 3, 4). This triangular patch forms the postero-median area of an enormous flap of fibrous and lamellar shell material apparently representing an extension of the posterior part of the pedicle valve and invariably sharply reflexed just dorsal of the base of the triangular lamellar layer. The shape of the flap varies considerably: specimens attached to a regular surface possess a flap which resembles a pair of expanded ears extending laterally from the median reflexed area (Pl. 2, Fig. 5); in those which lay free on the sea floor throughout most of their lives the flap is greatly extroverted so that the distal edge is usually in contact with the external surface of the pedicle valve (Pl. 2, Fig. 1); in those attached to irregular surfaces or crinoid stems the flap is closely adherent and moulded to the base (Pl. 2, Fig. 3); and in two distinct stocks, *Chaoella* and *Adriana*, the flap grew forward and is anky-

PLATE 2

FIG. 1.—Submedian portion of the posterior flap of *Oldhamina decipiens*, reconstructed from serial sections of BM. 18646, Permian, Salt Range, India: 1, 2, 3, 4, and 5 are successive layers of shell deposited by the posterior flap, the circles (R) represent the minimum point of retractibility of the mantle flap necessary for the deposition of each succeeding layer; D, dental area; L, lamellar layer; P, pseudopunctate fibrous layer; PV, pedicle valve; T, triangular area of lamellar calcite. (× 9)

FIG. 2.—Submedian view of interior of pedicle valve of *Chaoella* sp., Permian (Leonard) W. Texas: L, lamellar layer; P, pseudopunctate fibrous layer; PF, posterior flap; PV, pedicle valve; T, triangular area of lamellar calcite. (× 2.5)

FIGS. 3, 4.—Submedian and posterior views of the apical part of the pedicle valve of *Leptodus* sp., Permian (Word), Texas: D, dental area; L, lamellar layer; P, pseudopunctate fibrous layer; PF, posterior flap; PV, pedicle valve; R, reflexed region of posterior flap; T, triangular area of lamellar calcite. (× 3)

FIG. 5.—Apical part of pedicle valve of *Leptodus* sp., Permian (Word) Texas: D, dental area; PF, posterior flap; PV, pedicle valve. (× 3)

FIGS. 6, 7.—Portion of septal apparatus of *Leptodus* cf. *richthofeni* Kayser, Permian (Sosio), Sicily and *Oldhamina decipiens*, Permian, Salt Range, India respectively, reconstructed from serial sections: L, lamellar layer; F, pseudopunctate fibrous layer. (× 8)

FIG. 8.—Submedian view of a reconstruction of a *Leptodus* to show the relationship between the mantle and the shell (portrayed in solid black in section): C, cirrus of schizolophous lophophore; EM, exposed part of the ventral mantle lobe (M); IP, internal plate enveloped by an infold of the dorsal mantle lobe; PF, retractible posterior flap; V, visceral region.

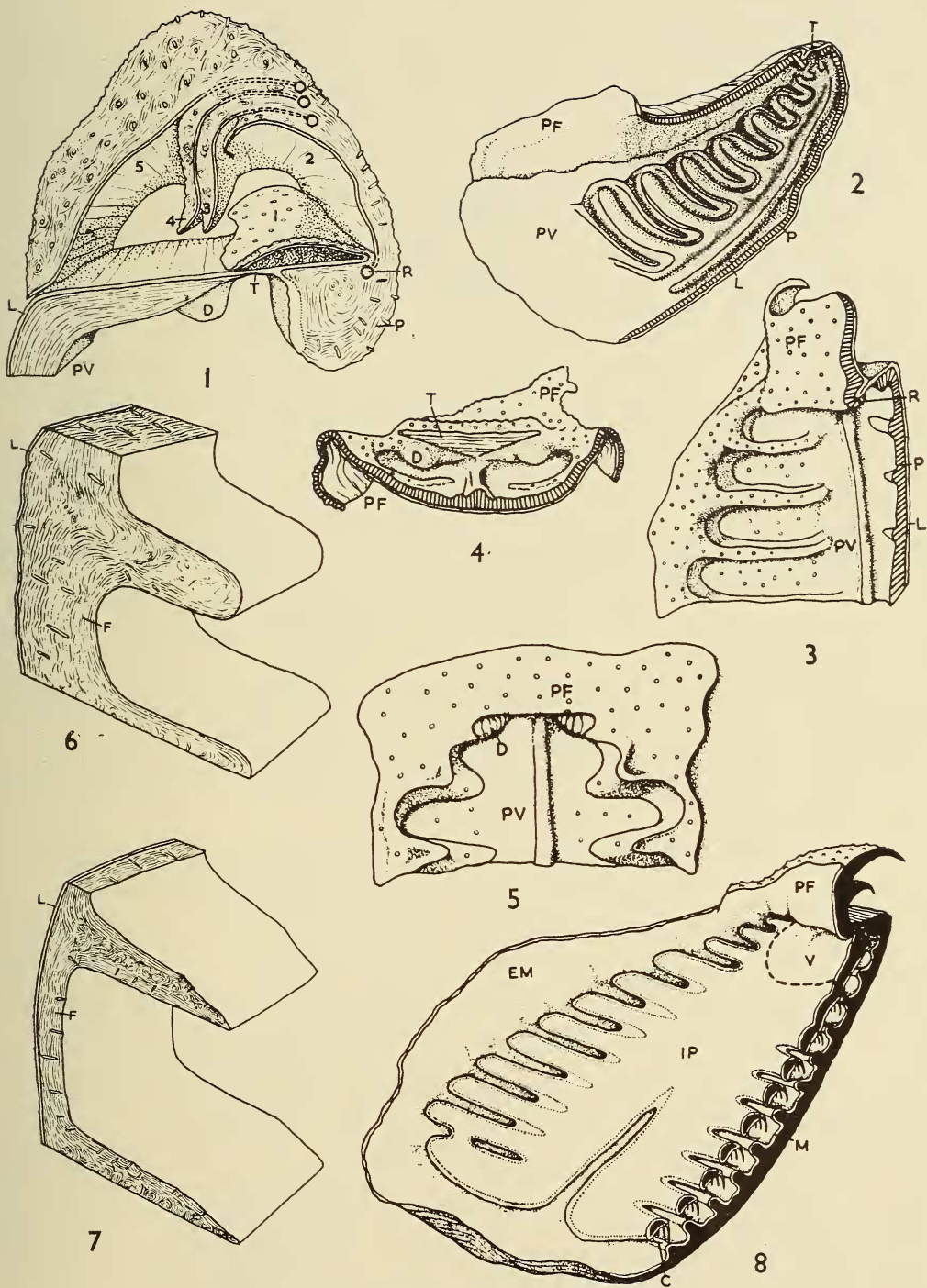


PLATE 2.— (See opposite page for legend).

losed to the sides of the pedicle valve to form a deep cone (Pl. 2, Fig. 2).

The posterior flap, although apparently an integral part of the pedicle valve, lies dorsal to the brachial valve and was the prime organ of fixation (indeed the only one in those oldhaminids attached to crinoid stems). It is envisaged as having been laid down by a posterior extension of the mantle capable of a rapid deposition of cementing shell material and disposed in such a way that the inner epithelial layer was invariably exposed. This posterior mantle flap was highly variable in shape, moulding itself closely to the base of attachment and it must be concluded that the mantle was greatly retractible so that paper-thin layers of shell consisting of both fibrous and lamellar calcite could be plastered one on top of another (Pl. 2, Fig. 1).

The origin of the posterior mantle flap is unknown, for no homologue is known to exist in other brachiopods; but it is a constant feature of all oldhaminids and is as prominent in primitive forms like *Poikilosakos* as it is in later Permian forms.

THE ARTICULATORY APPARATUS

If these conclusions on the form of the shell are acceptable it is not surprising to find that the leptodid articulatory apparatus is degenerate.

The cardinal process is undoubtedly bilobed but is usually rather inconspicuous in marked contrast to the pronounced development of the structure among strophomenoids generally. Anterolaterally to the cardinal process lie a pair of concave surfaces oval in outline and extending down to the first pair of lateral lobes. These surfaces are usually striated and represent sockets for the reception of a pair of similarly striated slightly convex surfaces (dental areas of Watson, 1917, p. 213) in the apical region of the pedicle valve.

The fact that the muscle scars are usually asymmetrically and sporadically impressed has been fully discussed by paleontologists. Well preserved interiors of the brachial valves sometimes bear a pair of variably defined impressions anterior to the cardinal process which have been taken to be the adductor scars. Occasionally too a full complement of diductor and adductor scars may be seen in the postero-median region of the interior of the pedicle valve (e.g., *Poikilosakos variabile* Wanner and Sieverts, 1935); and it

seems that the diductors, when normally disposed, were inserted in a pair of narrowly divergent depressed areas sometimes bounded by ridges and lying lateral to submedian adductor scars. These scars however are frequently unequally developed and asymmetrically disposed. In *Poikilosakos petaloides* Watson and *Oldhamina decipiens* (de Koninck) as figured by Noetling (1905) the left adductor scar is rudimentary compared with the right adductor and the right diductor appears to have atrophied: this indicates, according to Watson (1917, p. 215), that the brachial valve was moved laterally rather than dorsally in response to diductor contraction, although such movement must have been impossible in those oldhaminids having convex pedicle valves.

In general it is safe to assume that the oldhaminid musculature was degenerate to a degree of almost total atrophy and, although muscle fibres probably separated the epithelial layers of the mantle infold enveloping the internal plate, it is likely that the brachial structures were never elevated or slewed laterally as in normal brachiopods. This lack of movement was not detrimental to the living animal: the internal plate was elevated above the floor of the pedicle valve by the septal apparatus: a steady flow of nutrient water, circulated by the lobated lophophore, could have entered the brachial cavity by way of the distal ends of the lateral lobes and left by the median incision.

MORPHOGENY OF THE OLDHAMINID SEPTAL APPARATUS

The development of the septal apparatus in the oldhaminid pedicle valve corresponding to the lobation of the internal plate has been fully discussed by Fredericks (1925) and Wanner (1935) and needs but a brief review here.

In the primitive *Poikilosakos* a low ridge (flange of Watson, 1917), lying well within the pedicle valve margin completely surrounds the median area of the interior. The flange is roughly subcircular in outline and is indented to form a median loop only, but in adult forms the outline is more irregular, the flange being thrown into a small number of asymmetrically disposed lateral loops in addition to the median one. These loops are not greatly constricted and consequently include medianly a narrow strip of the valve floor bounded by an indented segment of the

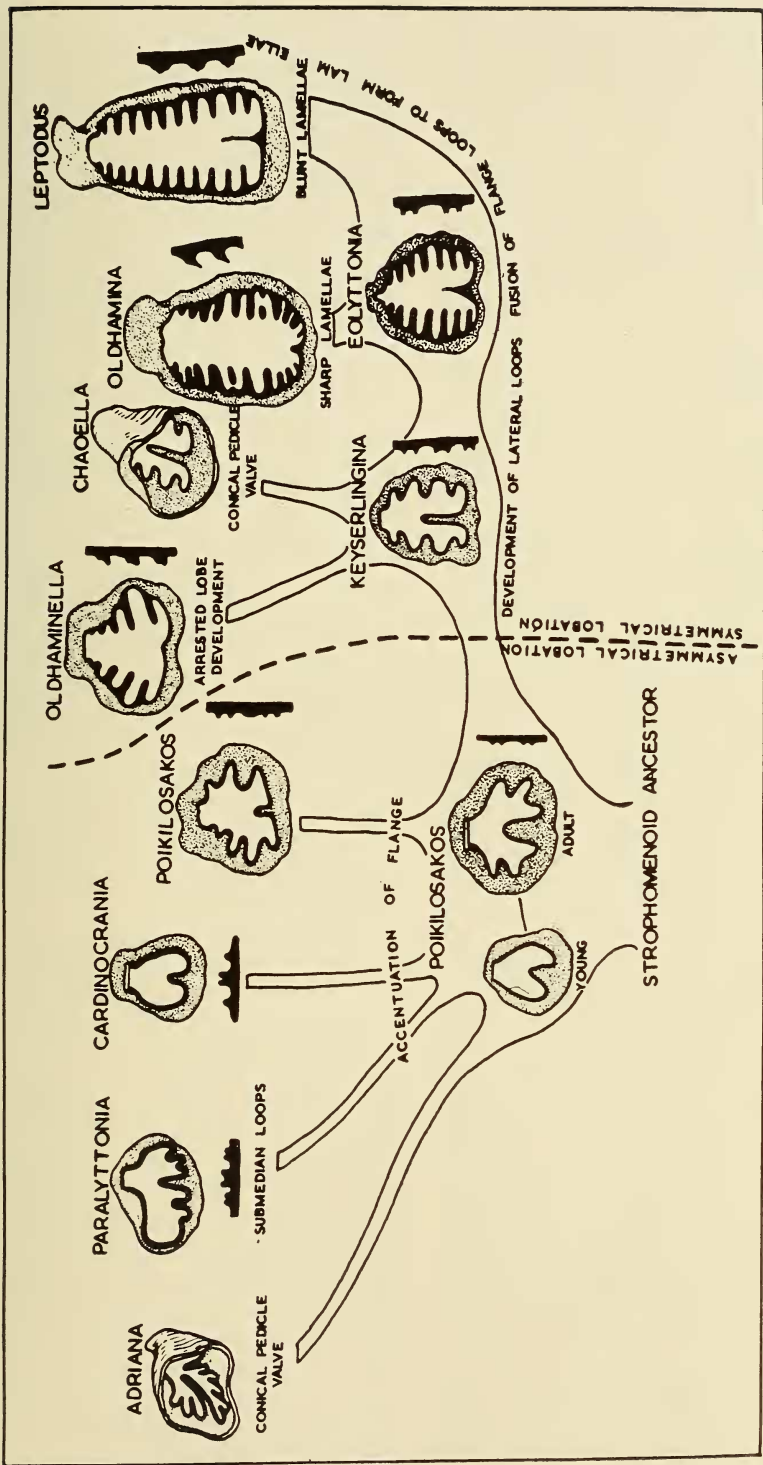


PLATE 3

Diagrammatic representation of oldhaminoid morphogeny; the profile of a representative portion of the loop or septal development in the pedicle valve of a genus is colored black.

flange. The internal plate of the brachial valve corresponds in outline to the disposition of the flange so that it is irregularly lobate and lies so close to the pedicle valve that each lobe is seemingly isolated distally from its neighbour by a loop of the pedicle valve.

In later oldhaminids like *Keyserlingina* and *Paralyttonia* the loops begin to close by an increase in the size of the flange boundaries and their encroachment onto the median strip of the valve floor until in extreme forms like *Oldhamina* and *Leptodus* the flange boundaries to each loop are completely united into one solid septal structure. In this manner the looped flange of the earlier and more generalized oldhaminids is transformed into a series of variously fashioned septa constituting the septal apparatus of more specialized stocks.

These views on the evolution of the septal apparatus are generally accepted but there seems to be disagreement on the systematic value of the modifications resulting from loop and septal morphogeny (see Wanner, 1935, pp. 265 et seq.) which appear to have been gradually introduced during the ontogeny of the various stocks as well as phylogenetically. Thus in one specimen of *Leptodus* from the Permian of Texas the high sharp septa of the earlier formed posterior region of the septal apparatus are replaced by lower, weaker septa in the later stages of growth, and the initially undifferentiated interseptal strips of the valve floor become elevated into low broad ridges in the anterior part of the shell. These changes were first introduced at the distal ends of the earlier formed septa and gradually encroached anteriorly on to the median line as the animal grew, in such a way that the changeover, which is quite sharply demarcated, occurred along a front convex to the anterior and roughly concentric with the growing edge of the valve.

Other modifications usually associated with the evolution of the septal apparatus included an increase in the number of septa and a closing up of the median incision of the internal plate; but the most important appears to have been a reorganisation of the disposition of loops and septa so that during Permian times two main stocks existed—one characterized by asymmetry the other by symmetry in the development of loops and septa.

OLDHAMINID CLASSIFICATION

The placing of the oldhaminids within the framework of the existing brachiopod classification has been a matter of considerable speculation. Fredericks (1925) considered the group to be derived from the productid *Marginifera*, but more accurate comparative morphology has caused the rejection of this belief. Other paleontologists including Waagen and Wanner have been impressed by the apparent similarity (especially in lobated nature of the lophophore support) between the oldhaminids and the theci-deids, and have considered them to be related groups. Both Watson and Noetling, however, have attributed the superficial likenesses to convergence and thus have regarded the stocks to be entirely independent, an opinion supported by the writer.

The various opinions expressed on the affinities of the oldhaminids is a reflection of the profound morphological differences separating them from all other brachiopods, and while most paleontologists place them within the strophomenoids no cogent reason has yet been put forward for allocating them either to the Strophomenoidea or to the Productoidea. That they are strophomenoids is left in little doubt when reference is made to the pseudopunctate shell, the absence of a functional pedicle and the presence of a bilobed cardinal process. But it is impossible to recognise in any of the Upper Carboniferous productoids and orthotetaceids any one stock displaying the characteristic oldhaminid features apart from the ordinal characters listed above. In view of these fundamental differences and the consequent unique nature of the oldhaminid morphology it is proposed to erect a new sub-order Oldhaminoidea to embrace *Oldhamina* and its associates.

The oldhaminoids include a wide variety of forms (Pl. 3) but appear to be divisible, as a result of a basic and early divergence, into two distinct suprageneric groups dependent upon the disposition of the septa and loops and it is proposed to recognise these differences by the erection of a new family, Poikilosakiidae, in the manner described below.

OLDHAMINOIDEA, n. suborder

Pseudopunctate brachiopods without a functional pedicle, usually cemented throughout ontogeny, shell surface without radial ornament,

shape often highly irregular. Brachial valve vestigial occupying a small posterior triangular area of a large plate of fibrous calcite presumed to have been deposited by an infold of the mantle and to have given support to a ptycholophous or more usually a schizolophous lophophore. Pedicle valve extending posteriorly as an enormous flap intimately connected with the pedicle valve apically and posterolaterally and invariably retroflexed along a narrow median zone lying immediately dorso-posteriorly to the brachial valve, posterior flap highly variable in form, usually the principal organ of fixation and moulded to the base affording anchorage, less frequently strongly retroflexed to come in contact with the external surface of the apical part of the pedicle valve or growing anteriorly and ankylosed to the sides of the pedicle valve to form with it a deep cone. In early stocks the median area of the pedicle valve interior surrounded by a low ridgelike flange indented to form a median loop and a variable number of lateral loops; in later stocks the sides of loops coalesced to form solid septa; internal plate of brachial valve lobated to correspond to the loops or septa. Upper Carboniferous to Permian.

Family OLDHAMINIDAE Schuchert and LeVene, 1929

Oldhaminoids with the loops or septa and hence the lobation of the brachial internal plate

symmetrically disposed about the median line. Upper Carboniferous to Permian. Type genus *Oldhamina* Waagen.

POIKILOSAKIDAE, n. fam.

Oldhaminoids with the loops or septa and corresponding lobes of the brachial internal plate developed in an irregular fashion. Upper Carboniferous to Permian. Type genus *Poikilosakos* Watson.

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ENTOMOLOGY.—*Additional material on the phylogeny and dispersal of Atopsyche (Trichoptera: Rhyacophilidae)*.¹ HERBERT H. ROSS, Illinois Natural History Survey, Urbana, Ill.

The intermingling of elements of South American and North American biotas across the Central American region is a study full of fascination. The fossil record for any terrestrial group in this critical area is very scanty, so that pertinent evidence from biogeography may be our best source of information on certain phases of the subject for some time to come.

Since Dr. King and I prepared our first paper on the dispersal pattern of the genus *Atopsyche*, known only from this area, I have been fortunate in obtaining several additional lots of material and in being

¹ This study was aided by a grant from the John Simon Guggenheim Memorial Foundation.

able to study the type of *A. implexa* (Navas). Although the new material adds only eight species to the 21 previously analyzed, it brings out several points of biogeographic interest. These fit well the concepts and postulates set forth in the earlier paper on the genus (Ross and King, 1952, Ann. Ent. Soc. Amer. **45**: 177-204) extending some ideas and suggesting modifications of others.

In the first place, the new species *ulmeri* from Peru is a close relative of *cira* from Costa Rica and demonstrates a spread of this otherwise northern group from Central America into South America. This was probably a post mid-Pliocene dispersal.